

Influence of tree-fall gaps on directional seed dispersal by small mammals in Central Panama

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Abstract

Small mammals, particularly rodents, are often important seed-dispersal agents in Neotropical forests. Directional seed dispersal into tree-fall gaps may enhance seedling survival of light-demanding species and thus influence forest regeneration. To examine this proposition, we tracked seeds of a light-demanding palm (*Attalea butyracea*), with a focus on spiny rats (*Proechimys semispinosus*), the most-likely seed-removal agents. We established seed-removal stations at three distances relative to 28 gaps (gap center, gap edge, and intact forest 10 m from a gap edge) in a lowland forest in Central Panama. We placed five fresh fruits (with their seed) in semi-permeable exclosures to exclude larger mammals at each station and tracked the directions in which seeds were moved and deposited intact. More seeds were moved toward or into gaps when removed from gap center or edge stations; however, seeds dispersed from intact forest stations showed no such directionality. Small mammals may have dispersed seeds into and within tree-fall gaps because they favored caching seeds in areas that offered increased cover, which is typical of gaps, and consequently protection from predation. The lack of directional dispersal from intact forest stations may have been because spiny rats were able to find sufficient cover in the young intact forest that was closer than the gaps. In older forest, the contrast between intact forest and gaps may be greater, resulting in directed dispersal into gaps.

Keywords

Attalea butyracea, directed dispersal, forest regeneration, *Proechimys semispinosus*, rodents, spiny rat

Introduction

Seed dispersal increases the fitness of plants by enabling escape from species-specific enemies and by allowing seeds to be moved into favorable sites (Janzen 1970; Connell 1971). While there are a variety of methods of seed dispersal, including gravity, wind, water, and phoresy, more than 66% of Neotropical canopy trees' seeds are dispersed when animals consume their fruits (Wunderle 1997). In cases such as wind, water, and phoresy, dispersal pathways are often random; by contrast, animal consumers may sometimes exhibit non-random or directed dispersal of seeds (Briggs et al. 2009; Dittel et al. 2015). If seeds are directionally dispersed into microhabitats that provide favorable germination and growing conditions, then the dispersal of seeds into such areas may increase tree fitness (Beckage et al. 2008; Briggs et al. 2009; Mason et al. 2022). Canopy gaps that are formed by tree-falls may create favorable microhabitats in which seedlings thrive because gaps often offer favorable sunlight, moisture, and temperature regimes and reduced competition with larger plants (Beckage et al. 2008; Briggs et al. 2009). Such gaps are particularly important for light-demanding plants, and areas with gaps invariably have higher plant species richness than areas without gaps (Denslow et al. 1990; Denslow and Hartshorn 1994; Kricher 1997).

Numerous studies have examined the role of larger mammals, such as agoutis and monkeys, in seed dispersal in Neotropical forests; however, few studies have examined seed dispersal by smaller mammals whose relative abundance and biomass may surpass those of larger species, especially in disturbed areas (Lambert et al. 2006; Carvajal and Adler 2008). Additionally, some species of small mammals, such as Central American spiny rats (*Proechimys semispinosus* (Tomes, 1860)), are known seed dispersers (Hoch and Adler 1997; Adler and Kestell 1998) that are associated with tree-fall gaps (Lambert and Adler 2000; Carvajal and Adler 2008). While it has been suggested that such small mammals may preferentially disperse seeds into tree-fall gaps (Carvajal and Adler 2008), this directed dispersal has not yet been verified. Such dispersal could influence the spatial distribution of plant species and ultimately tropical forest regeneration (Carvajal and Adler 2008; Briggs et al. 2009; Dittel et al. 2015). Understanding seed dispersal in tropical forests is particularly crucial because forest disturbance and fragmentation may alter dispersal networks (Emer et al. 2020), and anthropogenic disturbances are continuing unabated. We therefore hypothesized that smaller mammals such as spiny rats preferentially disperse seeds from the outside of a gap towards or into a gap. To test this hypothesis, we examined the movement of seeds of the light-demanding palm *Attalea butyracea* (Mutis ex. L.f.) in relation to tree-fall gaps in a lowland forest in Central Panama.

Methods

Study site

This study was conducted in Soberania National Park in Central Panama (9.1413, -79.7192, Fig. 1). The park is located near the junction of the Panama Canal and the



Figure 1. Map of the location of the study site in Soberania National Park, indicated by the red dot; darker green shading shows the area within the park boundaries. Inset shows the location in Central Panama, indicated by the red dot. Source: ISRI Base Maps, using ArcGIS Desktop version 10.82.

Chagres River and encompasses 22,104 ha of mostly second-growth forest, with some small patches of old-growth forest. Study plots were accessed by Pipeline Road, which is an unimproved track that runs from southeast to northwest through the park. This area of Panama experiences pronounced seasonality, having a four-month dry season from January through April and an eight-month wet season from May through December. This variation in precipitation leads to two distinct peaks in fruiting, the first between March and June and the second between September and October (Foster 1996).

Study system

Attalea butyracea is a common palm within lowland forests of the northern Neotropics and is particularly abundant in disturbed areas (Henderson et al. 1995). It reaches a height of 20 m and reliably produces one to four large infructescences every year (Adler and Lambert 2008). Fruits are consumed by many terrestrial and arboreal frugivorous mammals, and seeds are frequently preyed upon by bruchid beetles and rodents (Henderson et al. 1995).

Proechimys semispinosus (Fig. 2) is often the most abundant terrestrial rodent within lowland forests of the northern Neotropics, including in the study area



Figure 2. Adult *Proechimys semispinosus* from the study site. Photo credit: Ashley Winker.

(Tomblin and Adler 1998). This strictly-terrestrial echimyid rodent consumes a wide variety of fruits and seeds, including those of *A. butyracea* (Adler 1995). It also frequently scatter hoards large seeds (Hoch and Adler 1997; Adler and Kestell 1998; Carvajal and Adler 2008; Kilgore et al. 2010; Dittel et al. 2015).

Data sampling

Second-growth forest along the first 2 km at the southeast end of Pipeline Road was thoroughly searched for the presence of tree-fall gaps (Fig. 3a–d). We established three seed-removal stations at each gap, with one in the geometric center of a gap, one within 1 m of the gap edge (either inside or outside of the gap, hereafter referred to as gap edge), and one in intact forest 10 m from the gap edge (hereafter referred to as intact forest). The directions of the edge and intact forest stations from the center of the gap were randomly selected for each gap. Tomahawk live traps (41×13×13 cm, Tomahawk Trap Company, Tomahawk, WI, USA) were wired open to create semipermeable exclosures that excluded access to mammals larger than ca 1 kg, such as adult Central American agoutis (*Dasyprocta punctata* (Gray, 1842)). While these exclosures largely limited removals to *P. semispinosus* (the most abundant rodent in the study area, Adler et al. 1998; Tomblin and Adler 1998), we could

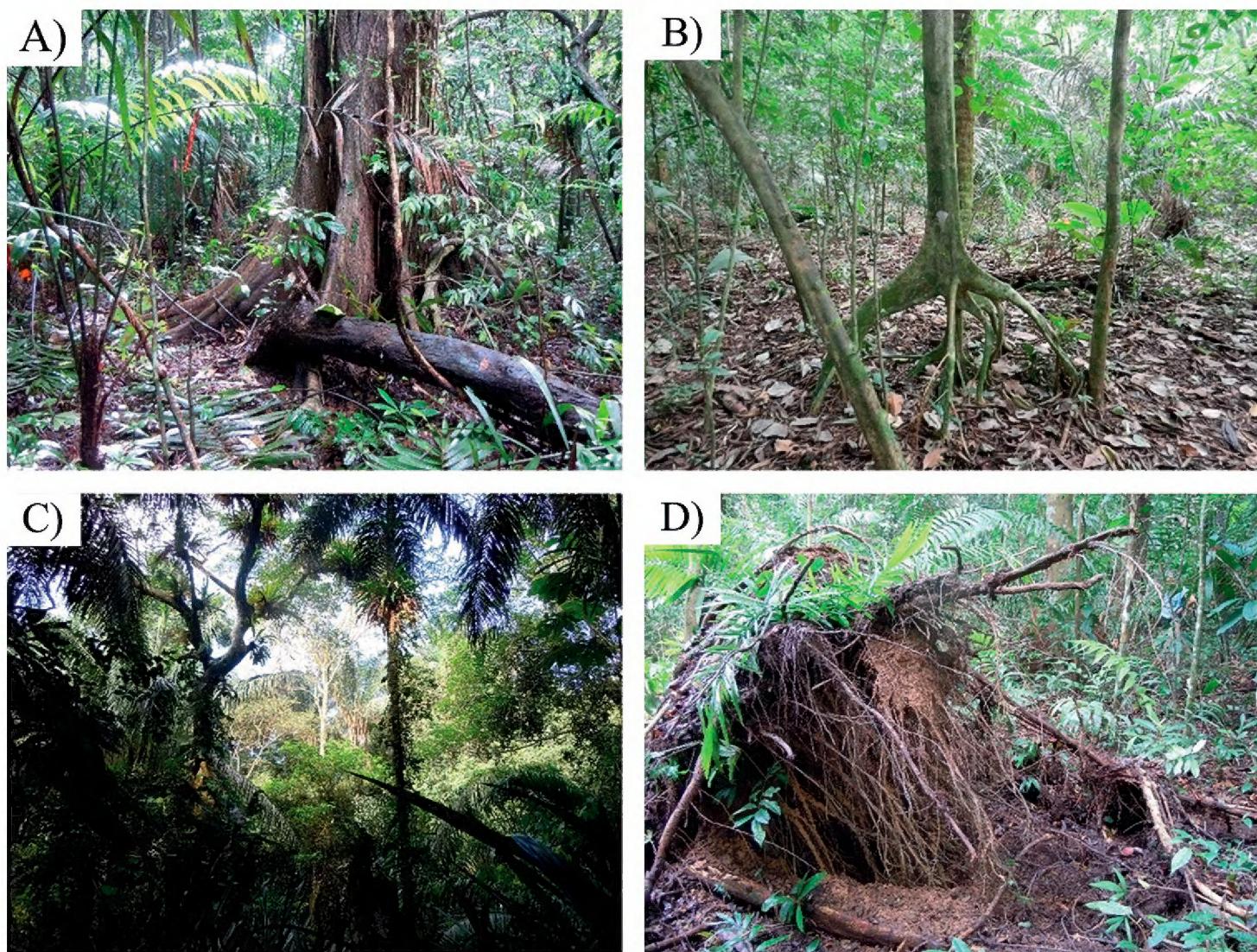


Figure 3. Intact forest (A, B) and gaps (C, D) within the study site. Photo credits: Ashley Winker.

not exclude red-tailed squirrels (*Sciurus granatensis* (Humboldt, 1811)); however, they were not as abundant as spiny rats, and they frequently transported seeds into trees (Carvajal and Adler 2008; Kilgore et al. 2010) rather than depositing them in gaps. We also could not exclude larger opossums that might occasionally feed on fruit, but they rarely transport large seeds (personal observations). Other rodents in the study area, such as Desmarest's spiny pocket mice (*Heteromys desmarestianus* Gray, 1868), were too small to transport *A. butyracea* seeds.

Seeds from *A. butyracea* with intact fresh mesocarp and ectocarp were collected, and holes were drilled in one end of each seed using a 1.2-mm drill bit. Such fruits range from 4.5–8.5 cm long and 3–4.5 cm in diameter and rely almost exclusively on animal dispersal (Henderson et al. 1995; Adler and Lambert 2008). Industrial sewing bobbins were wrapped in waterproof surgical tape to prevent the thread from snagging on vegetation during removal by the mammals. Thin annealed metal wire was then used to attach the seed with intact fresh fruit to the thread bobbin (e.g., Kilgore et al. 2010). Five seeds with intact fresh fruit and attached bobbins were placed in the exclosures at each seed removal station (i.e., 15 fruits per gap), and the free end of the bobbin thread was secured to the exclosure. Thus, when a mammal removed a seed from the exclosure, a thread trail remained, and the seed dispersal pathway was revealed. The exclosures at each gap were checked daily for

seed removals for a combined total of 49 days over the span of two wet seasons from June to August 2012 (13 gaps) and 2013 (15 gaps). In the event of a removal, the thread trail was used to identify the dispersal pathway and final location and fate of the seed. We included for further consideration only those seeds that were moved and deposited on the ground intact because seeds that were destroyed or deposited above ground did not constitute successful dispersal events. The distance and direction relative to the tree-fall gap associated with a given removed seed were measured and recorded. We examined the fruits in the exclosures daily and replaced any overly-ripe, moldy, or removed fruits.

Data analysis

We used χ^2 analysis to determine if the number of seeds dispersed differed from random dispersal expectations. To determine the expected number for each direction, we divided the area around a seed station into four hypothetical quadrants. Therefore, it was expected that 25% of the total removals would be dispersed toward the tree-fall gap, 25% would be dispersed away from the tree-fall gap, and 50% would be dispersed in directions parallel to the gap if the presence of the tree-fall gap was not affecting dispersal direction. This method was not applicable to analyze the direction of seeds dispersed from gap-center seed stations; therefore, the results for those stations are reported as percentages only. We used a mixed-effects analysis of variance (ANOVA) to determine if there was a difference in the distance that seeds were dispersed among tree-fall gaps or stations or between years.

Results

Over the span of two data-collection seasons, we tracked 282 removed and deposited seeds (71 in 2012 and 211 in 2013) at the 28 gaps. Of those, 116 were deposited less than 0.30 m from seed exclosures and therefore were not considered “dispersals” in this study. Additionally, 11 removals were taken into trees and were not included in the analysis. Dispersed seeds were typically deposited under leaf litter.

Of the 155 dispersed seeds, 114 were moved into or toward the tree-fall gap, 25 were moved in directions parallel to the gap, and 16 were moved away from the gap (Table 1). Of the 155 total dispersals, 75 were removed from seed stations located at the center of tree-fall gaps, where three (4.0%) were dispersed outside of the tree-fall gap, and the other 72 (96.0%) remained within the gap (Fig. 4). The χ^2 analysis showed that at seed stations at gap edges, more seeds were moved toward the gap ($\chi^2 = 33.84$, d.f. = 2, $P < 0.0001$) than would be expected if random dispersal were occurring. The number of dispersals in each direction at the intact forest stations were not different from the expected values ($\chi^2 = 4.31$, d.f. = 2, $P = 0.116$), indicating that directional dispersal, either into or away from a gap, was not occurring at that distance from the gap.

The mixed-effects ANOVA showed that there was no difference in dispersal distance among tree-fall gaps ($P = 0.143$, d.f. = 13) or between data collection years

Table 1. The number and percentage of seeds that were dispersed in each direction from each seed station location.

Station	Toward or into gap		Parallel to gap		Away from or into gap	
	Number	%	Number	%	Number	%
Center	72	96.0	-	-	3	4.0
Edge	33	57.9	13	22.8	11	19.3
10 m	9	39.1	12	52.2	2	8.7

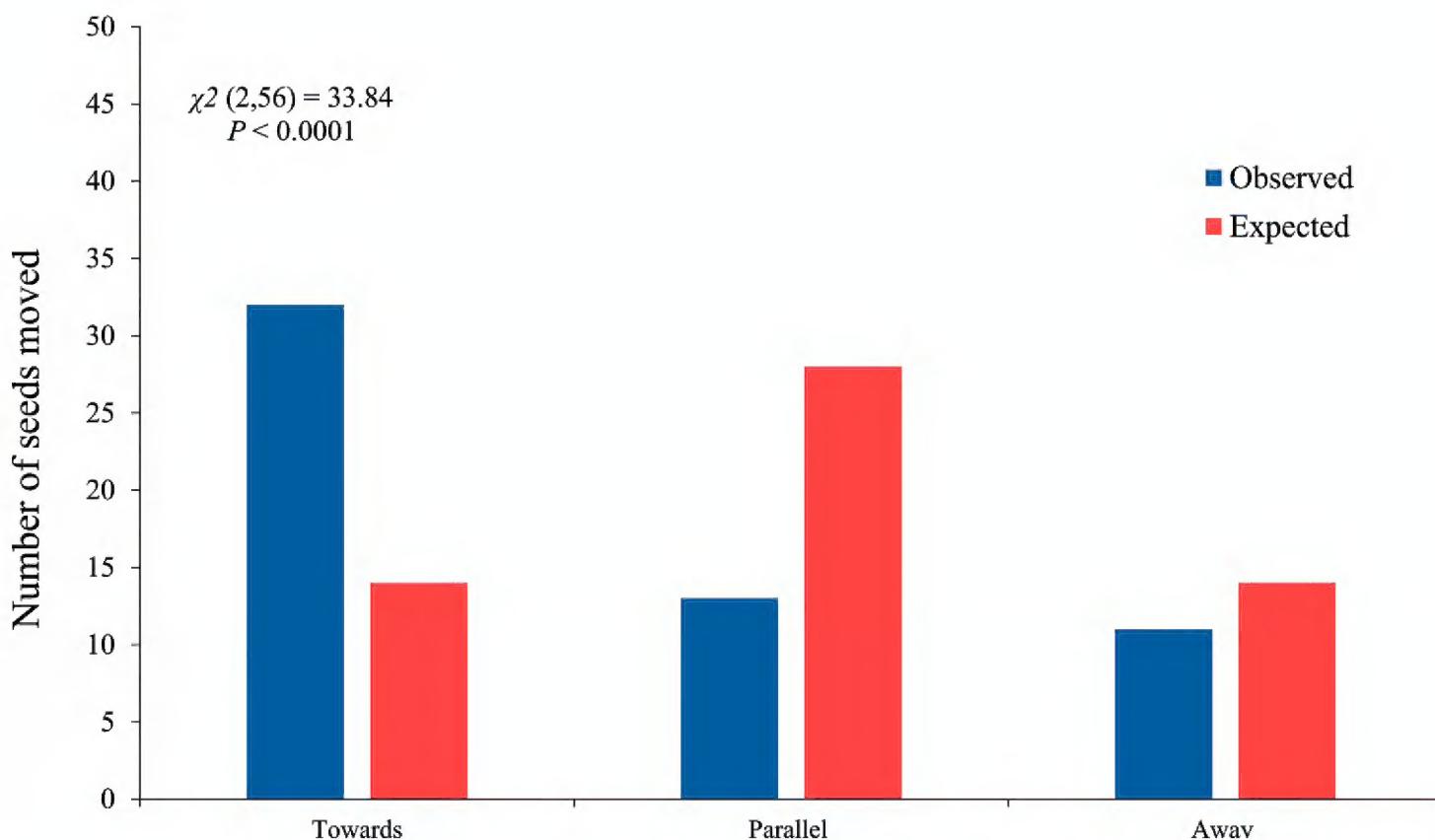


Figure 4. Comparison of observed versus expected of the number of seeds moved toward the tree-fall gap, in directions parallel to the gap, and moved away from the gap (χ^2 test, $\alpha = 0.05$).

($P = 0.745$, d.f. = 1). There was also no difference in dispersal distance between station locations ($P = 0.051$, d.f. = 151). Finally, there was no difference in dispersal distance between intact forest and edge stations ($P = 0.176$, d.f. = 151), nor between gap and edge stations ($P = 0.227$, d.f. = 151).

Discussion

Directed dispersal occurs when an animal safely transports a seed and deposits it in a nonrandom location that coincides with more favorable germination conditions. We hypothesized that small mammals such as *P. semispinosus*, because of their associations with tree-fall gaps and other disturbed areas of forest (Lambert and Adler 2000), might nonrandomly transport seeds of *A. butyracea* into gaps and cache them there if it does not consume them immediately. This nonrandom transport of seeds into high-light environments thereby potentially improves the germination and recruitment success of this light-demanding palm.

The presence of a tree-fall gap did indeed influence seed-dispersal direction by removal agents at gap center and edge locations. *Proechimys semispinosus*, in particular, may have directionally-dispersed seeds from center and edge locations within and into tree-fall gaps, respectively, due to its association with tree-fall gaps (Lambert and Adler 2000). This rodent may seek refuge in tree-fall gaps because the increase in structural complexity and cover from tree-fall debris and increased density of newly-recruiting light-demanding plants offer protection from predation while it consumes or caches seeds. Optimal foraging theory states that an animal should forage in a way that increases net energy intake and decreases the risk of predation (Lima et al. 1985; Dill 1987). In this scenario, *P. semispinosus* may expend energy carrying fruits and seeds to a safe area for consumption or storage (i.e., carrying a seed from the edge of a tree-fall gap into the complex structural architecture within the gap), but upon arriving at a safe location may consume or cache the seed with a decreased risk of predation. Cached seeds may therefore have enhanced germination and growth probabilities within the gap.

We found no such directional effect with seeds located in intact forest 10 m from a gap edge. This study was conducted in young, second-growth forest where the understory consisted of many structures, including patches of dense understory vegetation that could potentially offer protection from predators of small mammals, including *P. semispinosus*, while they consumed fruits or seeds or cached seeds. Center and edge stations were located at a tree-fall gap; therefore, individuals likely preferentially dispersed seeds in this direction because the closest structure offering safety was within a gap. However, as the distance from the gap increased, individuals needed to move seeds greater distances to find structures that provided safety. These structures may have been within the tree-fall gap but also could have included other structures within the surrounding second-growth forest if they were closer than the tree-fall gap. According to optimal foraging theory, small mammals should carry the seed to the closest structure that provided safety, whether it was within the tree-fall gap or in a different direction, which resulted in non-directional dispersal.

Our results suggest possibilities for future research to further understand the driving forces underlying directional seed dispersal into tree-fall gaps in Neotropical forests of various ages. While this study was conducted in a young, second-growth forest, the results may have differed if the study were conducted in old-growth forest where there is less cover near the ground in intact forest, and the structural contrast inside and outside of tree-fall gaps would be greater.

Conclusion

Our results demonstrate that small mammals such as spiny rats nonrandomly disperse seeds into tree-fall gaps if such seeds are already within or close to gaps. This directed dispersal may promote recruitment of light-demanding forest trees and consequently influence forest regeneration.

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